Competitive Exclusion for Chemostat Equations with Variable Yields

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Competitive exclusion for chemostat equations with variable yields*

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Abstract

In this paper, we study the global dynamics of a chemostat model with a single nutrient and several competing species. Growth rates are not required to be proportional to food uptakes. Our approach is based on the construction of Lyapunov functions. The Lyapunov functions extend those used by Hsu [SIAM J. Appl. Math. (1978) 34:760-763] and by Wolkowicz and Lu [SIAM J. Appl. Math. (1992) 57:1019-1043] in the case when growth rates are proportional to food uptakes. Our result generalizes a large variety of previous results obtained by Lyapunov techniques.
Keywords Chemostat, Competitive exclusion principle, Lyapunov function, Global asymptotic stability, Variable yield

1 Introduction and main result

The aim of this paper is to show that under certain conditions the Competitive Exclusion Principle (CEP) holds for the following competition for a single resource model

$$\begin{aligned} S' &= D[S^0 - S] - \sum_{j=1}^{N} p_j(S)x_j, \\ x_i' &= [q_i(S) - D_i]x_i, \qquad\qquad i = 1 \cdots N, \end{aligned} \tag{1}$$

where $S(t)$ and $x_i(t)$, $i = 1 \cdots N$, denote respectively the nutrient concentration and the concentration of the ith competing species at time t. The input concentration S^0 and the removal rates D and D_i are assumed to be constant. The uptake rate $p_i(S)$ satisfies

$$p_i(0) = 0 \text{ and } p_i(S) > 0 \text{ for } S > 0. \tag{2}$$

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The growth rate $q_i(S)$ satisfies

$$q_i(0) = 0 \text{ and } q_i(S) > 0 \text{ for } S > 0. \tag{3}$$

The functions $y_i(S)$, defined by

$$y_i(S) = \frac{q_i(S)}{p_i(S)}, \qquad i = 1 \cdots N, \tag{4}$$

are the growth yields. The model (1) was considered by Arino, Pilyugin and Wolkowicz [2] as an extension of the classical chemostat model

$$\begin{aligned} S' &= D[S^0 - S] - \sum_{i=1}^{N} \frac{q_i(S)}{Y_i} x_i, \\ x_i' &= [q_i(S) - D_i]x_i, \qquad i = 1 \cdots N, \end{aligned} \tag{5}$$

for which the yields $y_i(S) = Y_i$ are constant. The model (5) occupies a central place in mathematical ecology, see the monograph of Smith and Waltman [22]. It is a model of the dynamics of microbial competition. Basically, the chemostat consists of a nutrient input, pumped at a constant rate into a well-mixed culture vessel. The culture vessel contains the microorganisms that are growing and competing for the nutrient. Volume is kept constant by pumping the mixed contents out at the same rate. The smallest positive value of the concentration substrate $S = \lambda_i$ defined by the condition $q_i(S) = D_i$, where the growth $q_i(S)$ of x_i is balanced by the removal rate D_i is called the *break-even concentration* for the ith species.

Let us denote $f_i(S) = q_i(S) - D_i$, then (1) reduces to the model

$$\begin{aligned} S' &= D(S^0 - S) - \sum_{j=1}^{N} p_j(S)x_j \\ x_i' &= f_i(S)x_i, \qquad i = 1 \cdots N, \end{aligned} \tag{6}$$

considered by Fiedler and Hsu [7]. The growth rate $f_i(S)$ satisfies

$$f_i(S) < 0 \text{ for } 0 \le S < \lambda_i \text{ and } f_i(\lambda_i) = 0, \tag{7}$$

where λ_i are the break-even concentrations. Without loss of generality (see Section 2), we assume that $D = 1$ and $S^0 = 1$ in (6). The system becomes

$$\begin{aligned} S' &= 1 - S - \sum_{j=1}^{N} p_j(S)x_j, \\ x_i' &= f_i(S)x_i, \qquad i = 1 \cdots N. \end{aligned} \tag{8}$$

Coexistence of the N species is a fundamental question on the model (8) of competition for a single resource. Looking for coexistence at positive equilibria we have to solve equations $f_i(S) = 0$ simultaneously for all $i = 1 \cdots N$. In

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general, for $N \geq 2$, these equations cannot be solved for the same value of S. Thus, generically, (8) can have the following equilibria: the washout equilibrium

$$E_0 = (1, 0, \cdots, 0), \tag{9}$$

where all species go extinct, and equilibria E_i, $i = 1 \cdots N$, where all components of E_i vanish, except for the first and the $(i+1)$th, which are

$$S = S^*, \qquad x_i = \frac{1 - S^*}{p_i(S^*)},$$

where $S^* \in]0, 1[$ satisfies $f_i(S^*) = 0$. Hence, at any equilibrium point E_i, all but one species go extinct.

Since $f(\lambda_i) = 0$, the break-even concentration $S^* = \lambda_i$ gives rise to an equilibrium point E_i for the system, if and only if $\lambda_i < 1$. A well-known open-problem in the theory of the chemostat is to prove the global asymptotic stability of the equilibrium point E_i with the lowest break-even concentration. If this equilibrium is globally asymptotically stable (GAS), then the CEP holds: only one species survives, namely the species which makes optimal use of the resource. The reader is referred to [23], for complements and details on the CEP. Most of the results on the CEP for (1) and (5) have been based on Lyapunov functions [3, 9, 14, 20, 21, 25, 26] . For a survey of constructing Lyapunov functions in the chemostat, the reader is referred to [10]. We simply recall here that Hsu [9] proved the CEP for the Monod case of (5), when the growth functions are

$$q_i(S) = \frac{a_i S}{b_i + S}, \tag{10}$$

and Wolkowicz and Lu [25] extended the result of [9] to (5) with more general growth functions.

Instead of a Lyapunov function approach, Fiedler and Hsu [7] applied a multi-dimensional Bendixon-Dulac criterion to exclude periodic solutions. Under some technical conditions on the functions f_i and p_i they proved that (8) does not possess positive non-stationary periodic orbits. In our previous works [20, 21], we showed that both Lyapunov functions used by Hsu [9] and Wolkowicz and Lu [25] can be extended to the variable yields case model (1). The aim of this paper is to show that these Lyapunov functions can also be used to obtain the CEP for (8).

A necessary condition to avoid washout of the species, and global convergence towards the washout equilibrium E_0 defined by (9), is that $\lambda_i < 1$ for at least one species. Assume that the species are labeled so that $0 < \lambda_1 < 1$. Then

$$E_1^* = (\lambda_1, x_1^*, 0, \cdots, 0), \tag{11}$$

where $x_1 = x_1^* = P_1(\lambda_1)$ is an equilibrium. Here

$$P_1(S) = \frac{1 - S}{p_1(S)}. \tag{12}$$

Using linearization of (8) about E_1^* one proves that:

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Lemma 1. *The equilibrium (11) is locally exponentially stable if and only if* $f_1'(\lambda_1) > 0$ *and* $P_1'(\lambda_1) < 0$.

We consider the global asymptotic stability of E_1^*. Our main result is

Theorem 1. *Assume that (2) and (7) hold. Assume that* $\lambda_1 < 1$ *and for all* $0 < S < 1$,

$$(S - \lambda_1) f_1(S) > 0, \text{ for } S \neq \lambda_1, \tag{13}$$

$$(S - \lambda_1)(P_1(S) - P_1(\lambda_1)) < 0, \text{ for } S \neq \lambda_1, \tag{14}$$

where $P_1(S)$ *is defined by (12). Assume that there exist constants* $\alpha_i > 0$ *for each* $i \geq 2$ *satisfying* $\lambda_i < 1$, *such that for all* $0 < S < 1$,

$$f_1(S) p_i(S) > \alpha_i f_i(S)(1 - S). \tag{15}$$

Then the equilibrium E_1^* *is GAS for (8) with respect to the interior of the positive cone.*

The proof is given in Section 3. Notice that the following property holds.

Lemma 2. *The conditions* $\lambda_1 < 1$ *and (15) imply that* $\lambda_1 < \lambda_i$ *for all* $i \geq 2$.

Proof. Assume that there exists $i \geq 2$ such that $\lambda_i < \lambda_1$. Then, there exists $S \leq \lambda_1$ such that $f_i(S) > 0$. Hence, since $S \leq \lambda_1 < 1$, $f_i(S)(1 - S) > 0$. On the other hand, using (7), $f_1(S) \leq 0$. Hence, the inequality (15) is violated. □

This lemma shows that the winning species x_1 of Theorem 1 has the lowest break-even concentration, in accordance with the CEP for models of competition for a single resource [23].

The paper is organized as follows. In Section 2 we give some preliminary lemmas. In Section 3 we show how the Lyapunov function of Wolkowicz and Lu [25] can be extended to (8) and used to obtain Theorem 1. We show in this section that the result of [20] for (1), which extends the result of [25] for (5), is a corollary of Theorem 1. We give also graphical interpretations of the conditions (13), (14) and (15). In Section 4, we show how the Lyapunov function of Hsu [9] can be extended to (8) and used to obtain Theorem 2, which is another global asymptotic stability result of E_1^* for (8). Theorem 2 can be obtained also as a corollary of Theorem 1 (see Proposition 1). We show in this section that the result of [9] for (5) with Monod functions (10), and the result of [21] for (1) are corollaries of Theorem 2. In Section 5 we discuss the single species case $N = 1$. In Section 6 we apply our result to the model with Monod growth functions (10) and linear yields. In Section 7 we discuss some of the CEP results based on Lyapunov functions and we compare Theorem 1 with the results of [7] based on a Bendixon-Dulac approach.

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2 Preliminary results

Let us prove first that we can we assume that $D = 1$ and $S^0 = 1$ in (6). Indeed, under the change of variables

$$\overline{S} = \frac{S}{S^0}, \qquad \overline{t} = Dt, \qquad \overline{p}_i(\overline{S}) = \frac{p_i(S^0\overline{S})}{S^0 D}, \qquad \overline{f}_i(\overline{S}) = \frac{f_i(S^0\overline{S})}{D},$$

equations (6) take the form

$$\begin{aligned} \frac{d\overline{S}}{d\overline{t}} &= \frac{1}{S^0 D}\frac{dS}{dt} &&= 1 - \overline{S} - \sum_{j=1}^{N} \overline{p}_j(\overline{S})x_j, \\ \frac{dx_i}{d\overline{t}} &= \frac{1}{D}\frac{dx_i}{dt} &&= \overline{f}_i(\overline{S})x_i, \qquad\qquad i = 1 \cdots N. \end{aligned}$$

Dropping the bars, one obtains (8). Recall that $f_i(0) < 0$, so that the concentration of the species x_i is decreasing when the concentration of nutrient is too small. The smallest positive zero $S = \lambda_i$ of f_i is the break-even concentration of the ith species x_i. We adopt the convention $\lambda_i = \infty$ if $f_i(S) < 0$ for all $S > 0$. We need the following lemmas.

Lemma 3. *The non-negative cone is invariant under the flow of (8) and all solutions are defined and remain bounded for all $t \geq 0$.*

This lemma is simply Theorem 4.1 in [2].

Lemma 4. *If for some species x_i, the inequality $(S - \lambda_i)f_i(S) > 0$ is satisfied for all $0 < S < 1$, $S \neq \lambda_i$, then $S(t) < 1$ for all sufficiently large t and all initial condition .*

This lemma can be obtained using arguments similar to that given in the proofs of Lemma 2.9 in [2] and Lemma 2.1 in [25].

Lemma 5. *For all solutions of (8), if $\lambda_i \geq 1$ then $x_i(t) \to 0$ as $t \to \infty$.*

This lemma can be obtained using arguments similar to that given in the proofs of Lemma 4.2 in [2] and Lemma 2.2 in [25].

3 Extension of the Lyapunov function of Wolkowicz and Lu

The Lyapunov function used by Wolkowicz and Lu [25] in the constant yields case (5) is

$$V_{WL} = \frac{S^0 - \lambda_1}{D_1}\int_{\lambda_1}^{S} \frac{q_1(\sigma) - D_1}{S^0 - \sigma}d\sigma + \frac{1}{Y_1}\int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi}d\xi + \sum_{i=2}^{N} \frac{c_i}{Y_i}x_i. \qquad (16)$$

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with suitable constant $c_i > 0$. Using the notations in (8), and since S^0 was rescaled to 1, the function in the first integral of (16) is simply equal to $\frac{f_1(\sigma)}{1-\sigma}$. Multiplying (16) by the constant $\frac{D_1}{1-\lambda_1} = \frac{Y_1}{x_1^*}$, gives the following function

$$V = \int_{\lambda_1}^{S} \frac{f_1(\sigma)}{1-\sigma} d\sigma + \frac{1}{x_1^*} \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^{N} \alpha_i x_i, \tag{17}$$

where α_i are constants to be determined. This is a Lyapunov function for (8) which permits to prove Theorem 1 as shown below.

Proof. (*Theorem 1*) From Lemmas 4 and 5 it follows that there is no loss of generality to assume that $\lambda_i < 1$ for $i = 1 \cdots N$ and to restrict our attention to $0 < S < 1$. Consider the function $V = V(S, x_1, \cdots, x_N)$ given by (17) where α_i are positive constants satisfying (15). The function V is continuously differentiable for $0 < S < 1$ and $x_i > 0$ and positive except at point E_1^*. The derivative of V along the trajectories of (8) is

$$V' = \frac{f_1(S)}{1-S} S' + \frac{x_1 - x_1^*}{x_1^* x_1} x_1' + \sum_{i=2}^{N} \alpha_i x_i'.$$

Since $x_1^* = P_1(\lambda_1)$ and using (8), V' is written

$$V' = \frac{f_1(S)}{1-S} \left[1 - S - \sum_{i=1}^{N} p_i(S) x_i \right] + \frac{1}{P_1(\lambda_1)} [x_1 - P_1(\lambda_1)] f_1(S) + \sum_{i=2}^{N} \alpha_i f_i(S) x_i.$$

The terms $\frac{f_1(S)}{1-S}(1-S)$ and $-\frac{1}{P_1(\lambda_1)} P_1(\lambda_1) f_1(S)$ are canceled. Hence, using (12),

$$V' = x_1 f_1(S) \left[\frac{1}{P_1(\lambda_1)} - \frac{1}{P_1(S)} \right] + \sum_{i=2}^{N} x_i \frac{\alpha_i f_i(S)(1-S) - f_1(S) p_i(S)}{1-S}.$$

Using (13) and (14), the first term of the above sum is non-positive for $0 < S < 1$ and equals 0 if and only if $S = \lambda_1$ or $x_1 = 0$. Using (15), the second term is non-positive for $0 < S < 1$ and equals 0 if and only if $x_i = 0$ for $i = 2 \cdots N$. Hence $V' \leq 0$ and $V' = 0$ if and only if $x_i = 0$ for $i = 1 \cdots N$ or $S = \lambda_1$ and $x_i = 0$ for $i = 2 \cdots N$. Using the Krasovskii-LaSalle extension theorem, the ω-limit set of the trajectory is E_1^*. □

Theorem 1 was previously obtained in [20], in the particular case when the function f_i has at most two positive zeros λ_i and μ_i, with $\lambda_i \leq \mu_i \leq +\infty$, such that

$$f_i(S) < 0 \text{ if } S \notin [\lambda_i, \mu_i], \text{ and } f_i(S) > 0 \text{ if } S \in]\lambda_i, \mu_i[, \tag{18}$$

with the convention that $\mu_i = \infty$ if equation $f_i(S) = 0$ has only one solution and $\lambda_i = \infty$ if it has no solution. This class of functions corresponds to the case when $f_i(S) = q_i(S) - D_i$ and

$$q_i(S) < D_i \text{ if } S \notin [\lambda_i, \mu_i], \text{ and } q_i(S) > D_i \text{ if } S \in]\lambda_i, \mu_i[.$$

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It was often considered in the literature [4, 14, 25, 26]. For this class of systems the main result in [20] is

Corollary 1 (Theorem 2.1 in [20])**.** *Assume that (2), (7) and (18) hold. Assume that*

$$\lambda_1 < \lambda_2 \leq \cdots \leq \lambda_N, \text{ and } \lambda_1 < 1 < \mu_1, \tag{19}$$

$$(S - \lambda_1)(P_1(S) - P_1(\lambda_1)) < 0, \text{ for } S \neq \lambda_1, \tag{20}$$

where $P_1(S)$ is defined by (12). Assume that there exist constants $c_i > 0$ for each $i \geq 2$ satisfying $\lambda_i < 1$, such that

$$\max_{0<S<\lambda_1} h_i(S) < c_i < \min_{\lambda_i<S<\rho_i} h_i(S), \tag{21}$$

where $h_i(S) = \frac{1-\lambda_1}{p_1(\lambda_1)} \frac{f_1(S)p_i(S)}{f_i(S)(1-S)}$ and $\rho_i = \min(\mu_i, 1)$. Then the equilibrium E_1^* is GAS for (8) with respect to the interior of the positive cone.

Proof. Assume that (19), (20) and (21) hold. Let us prove that (13), (14) and (15) hold. First, note that (20) is the same as (14), and condition $\lambda_1 < 1 < \mu_1$ in (19) is equivalent to (13). If $\lambda_1 < S < \lambda_i$ then $f_i(S) < 0$ and $f_1(S) > 0$ so that (15) is satisfied for any choice of $\alpha_i > 0$. Similarly if $\mu_i < 1$ and $\mu_i < S < 1$ then $f_i(S) < 0$ and $f_1(S) > 0$ so that (15) is satisfied for any choice of $\alpha_i > 0$. On the other hand, if $0 < S < \lambda_1$ then $f_i(S) < 0$ and, using $h_i(S) < c_i$ in (21),

$$f_1(S)p_i(S) > c_i \frac{p_1(\lambda_1)}{1-\lambda_1} f_i(S)(1-S).$$

Finally, if $\lambda_i < S < \rho_i$, then $f_i(S) > 0$ and, using $h_i(S) > c_i$ in (21),

$$f_1(S)p_i(S) > c_i \frac{p_1(\lambda_1)}{1-\lambda_1} f_i(S)(1-S).$$

Thus (15) is satisfied for $\alpha_i = c_i \frac{p_1(\lambda_1)}{1-\lambda_1}$. The result follows from Theorem 1. □

Condition (13) means that $S = \lambda_1$ is the only zero of the growth function $f_1(S)$ for $0 < S < 1$. Condition (14) means that $S = \lambda_1$ is the only zero of the function $P_1(S)$ given by (12), for $0 < S < 1$. The technical condition (15) is trivially satisfied in the single species $N = 1$. Following [21, 25] we give now a graphical interpretation of (15). For each $i \geq 2$ such that $\lambda_i < 1$, consider the function

$$g_i(S) = \frac{f_i(S)}{f_1(S)} \frac{1-S}{p_i(S)}. \tag{22}$$

The functions g_i is defined on $(0, \lambda_1) \cup (\lambda_1, 1]$. It tends to $\pm\infty$ when S tends λ_1. Notice that the function h_i in Corollary 1 is simply a multiple of the reciprocal of g_i. We use g_i instead of h_i, since the zeros of f_i on $[0, 1]$ are not known as for the class of functions f_i considered in Corollary 1. Since $f_1(S) < 0$ over $[0, \lambda_1)$ and $f_1(S) > 0$ over $[\lambda_i, 1]$, the condition (15) is equivalent to

$$\min_{0<S<\lambda_1} g_i(S) > \frac{1}{\alpha_i} > \max_{\lambda_i<S<1} g_i(S). \tag{23}$$

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Hence, the condition (15) in Theorem 1 can be easily depicted graphically: plot simply the graph of $g_i(S)$ over $[0,1]$ and see if there is a gap between $\min_{0<S<\lambda_1} g_i(S)$ and $\max_{\lambda_i<S<1} g_i(S)$, see Fig. 5.

It was shown in [20] that the main result (Theorem 2.3) of [25] is a consequence of Corollary 1. Hence, it is also a corollary of Theorem 1.

4 Extension of the Lyapunov function of Hsu

The Lyapunov function V_H used by Hsu [9] in the Monod case of (5), where the growth functions are of the form (10), is

$$V_H = \int_{\lambda_1}^{S} \frac{\sigma-\lambda_1}{\sigma} d\sigma + c_1 \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^{N} c_i x_i, \tag{24}$$

with constants

$$c_i = \frac{1}{Y_i} \frac{a_i}{a_i - D_i}, \quad i = \cdots N, \quad \text{and } \lambda_1 = \frac{b_1 D_1}{a_1 - D_1}.$$

It is readily checked that the function in the first integral of (24) is given by $\frac{S-\lambda_1}{S} = c_1 \frac{f_1(S)}{p_1(S)}$, where

$$f_1(S) = \frac{a_1 S}{b_1 + S} - D_1, \qquad p_1(S) = \frac{1}{Y_1} \frac{a_1 S}{b_1 + S}.$$

Hence, multiplying (24) by the constant $1/c_1$ gives the following function

$$V = \int_{\lambda_1}^{S} \frac{f_1(\sigma)}{p_1(\sigma)} d\sigma + \int_{x_1^*}^{x_1} \frac{\xi - x_1^*}{\xi} d\xi + \sum_{i=2}^{N} c_i x_i. \tag{25}$$

where the constants c_i/c_1 in the last sum are simply denoted by c_i to avoid unnecessary new notations. Under some technical conditions, this function is a Lyapunov function for (8) and permits to obtain the global asymptotic stability of the equilibrium point E_1^* as stated in the following result.

Theorem 2. *Assume that (2) and (7) hold. Assume that $\lambda_1 < 1$ and for all $0 < S < 1$,*

$$(S-\lambda_1) f_1(S) > 0, \text{ for } S \neq \lambda_1, \tag{26}$$

$$(S-\lambda_1)(P_1(S) - P_1(\lambda_1)) < 0, \text{ for } S \neq \lambda_1, \tag{27}$$

where $P_1(S)$ is defined by (12). Assume that there exist constants $c_i > 0$ for each $i \geq 2$ satisfying $\lambda_i < 1$, such that for all $0 < S < 1$,

$$f_1(S) p_i(S) > c_i f_i(S) p_1(S). \tag{28}$$

Then the equilibrium E_1^* is GAS for (8) with respect to the interior of the positive cone.

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Proof. From Lemmas 4 and 5 it follows that there is no loss of generality to assume that $\lambda_i < 1$ for $i = 1 \cdots N$ and to restrict our attention to $0 < S < 1$. Consider the function $V = V(S, x_1, \cdots, x_N)$ given by (25) where c_i are positive constants satisfying (28). The function V is continuously differentiable in the positive cone and positive except at point E_1^*, where it is equal to 0. The derivative of V along the trajectories of (8) is

$$V' = \frac{f_1(S)}{p_1(S)} S' + \frac{x_1 - x_1^*}{x_1} x_1' + \sum_{i=2}^{N} c_i x_i'.$$

Since $x_1^* = P_1(\lambda_1)$ and, using (8), V' is written

$$V' = \frac{f_1(S)}{p_1(S)} \left[1 - S - \sum_{i=1}^{N} p_i(S) x_i \right] + [x_1 - P_1(\lambda_1)] f_1(S) + \sum_{i=2}^{N} c_i f_i(S) x_i.$$

The terms $-\frac{f_1(S)}{p_1(S)} p_1(S) x_1$ and $x_1 f_1(S)$ are canceled. Therefore, using (12),

$$V' = f_1(S) \left[P_1(S) - P_1(\lambda_1) \right] + \sum_{i=2}^{N} x_i \frac{c_i f_i(S) p_1(S) - f_1(S) p_i(S)}{p_1(S)}.$$

Using (26) and (27), the first term of the above sum is non-positive for $0 < S < 1$ and equals 0 if and only if $S = \lambda_1$. Using (28), the second term is non-positive for $0 < S < 1$ and equals 0 if and only if $x_i = 0$ for $i = 2 \cdots N$. Hence $V' \leq 0$ and $V' = 0$ if and only if $S = \lambda_1$ and $x_i = 0$ for $i = 2 \cdots N$. By the Krasovskii-LaSalle extension theorem, the ω-limit set of the trajectory is E_1^*. □

We have the following property.

Lemma 6. *The conditions $\lambda_1 < 1$ and (28) imply that $\lambda_1 < \lambda_i$ for all $i \geq 2$.*

Proof. If $f_i(S) > 0$ for some $S \leq \lambda_1$, then $f_1(S) \leq 0$, so that the inequality (28) is violated. □

This lemma shows that the winning species x_1 in Theorem 2 has the lowest break-even concentration. Actually Theorem 2 is a consequence of Theorem 1.

Proposition 1. *Theorem 2 is a corollary of Theorem 1.*

Proof. Assume that (26), (27) and (28) hold. Notice that (26) is the same as (13) and (27) is the same as (14). Let us prove that (15) holds. If $f_i(S) < 0$ and $f_1(S) > 0$ (which occurs if $\lambda_1 < S < \lambda_i$ and may occur also for $\lambda_i < S < 1$), then (15) holds for any choice of $\alpha_i > 0$. If $0 < S < \lambda_1$ then, by (27), $P_1(S) > P_1(\lambda_1)$ and, since $f_i(S) < 0$, $\frac{f_i(S)}{P_1(S)} > \frac{f_i(S)}{P_1(\lambda_1)}$. Finally, if $\lambda_i < S < 1$ and $f_i(S) > 0$ then, by (27), $P_1(S) < P_1(\lambda_1)$, and hence, $\frac{f_i(S)}{P_1(S)} > \frac{f_i(S)}{P_1(\lambda_1)}$. Therefore, in both cases $\lambda_i < S < 1$ and $0 < S < \lambda_1$,

$$\frac{f_i(S)}{P_1(S)} > \frac{f_i(S)}{P_1(\lambda_1)}.$$

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Thus, using (28),

$$f_1(S)p_i(S) > c_i f_i(S)p_1(S) = c_i \frac{f_i(S)}{P_1(S)}(1-S) > c_i \frac{f_i(S)}{P_1(\lambda_1)}(1-S).$$

Thus, (15) holds for $\alpha_i = \frac{c_i}{P_1(\lambda_1)}$. Hence, (27) and (28) imply (15). □

Theorem 2 recovers the classical case Monod case [9]. Indeed, consider the particular case of (5), when the growth functions $q_i(S)$ are given by (10). System (5), with $D = 1$ and $S^0 = 1$, takes the form

$$\begin{aligned} S' &= 1 - S - \sum_{j=1}^{N} \frac{a_j S}{b_j + S} \frac{x_j}{Y_j}, \\ x_i' &= \left[\frac{a_i S}{b_i + S} - D_i \right] x_i, \qquad\qquad i = 1 \cdots N. \end{aligned} \tag{29}$$

We consider the case where, for all $i = 1 \cdots N$, $a_i > D_i$. The break-even concentrations are

$$\lambda_i = \frac{b_i D_i}{a_i - D_i}. \tag{30}$$

Corollary 2 (Theorem 3.3 in [9])**.** *Assume that*

$$\lambda_1 < \lambda_2 \leq \cdots \leq \lambda_N, \qquad \lambda_1 < 1. \tag{31}$$

Then the equilibrium E_1^* is GAS for (29) with respect to the interior of the positive cone.

Proof. Assume that (31) holds. Let us prove that (26), (27) and (28) hold. Since $f_1(S) = q_1(S) - D_1$ is increasing, the function $f_1(S)$ changes sign only at $S = \lambda_1$ and hence, (26) is satisfied. Since

$$P_1(S) = Y_1(1-S)\frac{b_1 + S}{a_1 S} \qquad \text{and} \qquad P_1'(S) = -Y_1 \frac{S^2 + b_1}{a_1 S^2} < 0,$$

the function $P_1(S)$ changes sign only at $S = \lambda_1$ and hence (27) is satisfied. Condition (28) is

$$\frac{(a_1 - D_1)S - b_1 D_1}{b_1 + S} \frac{1}{Y_i} \frac{a_i S}{b_i + S} > c_i \frac{(a_i - D_i)S - b_i D_i}{b_i + S} \frac{1}{Y_1} \frac{a_1 S}{b_1 + S}, \qquad i \geq 2.$$

After simplification by $\frac{S}{(b_1+S)(b_i+S)}$, this condition is equivalent to

$$(a_1 - D_1)\frac{a_i}{Y_i}(S - \lambda_1) > c_i(a_i - D_i)\frac{a_1}{Y_1}(S - \lambda_i) \qquad i \geq 2, \tag{32}$$

which is satisfied for $c_i = \frac{(a_1 - D_1)a_i Y_1}{(a_i - D_i)a_1 Y_i}$. Indeed, for this choice of the constants c_i, (32) is simply

$$S - \lambda_1 > S - \lambda_i \Longleftrightarrow \lambda_1 < \lambda_i, \qquad i \geq 2,$$

which is the same as (31). Thus (28) is satisfied. The global asymptotic stability of E_1^* follows from Theorem 2. □

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Theorem 2 was previously obtained in [21], in the particular case when the function f_i satisfies (18). For this class of systems the main result in [21] is

Corollary 3 (Theorem 2 in [21]). *Assume that (2), (7) and (18) hold. Assume that*

$$\lambda_1 < \lambda_2 \leq \cdots \leq \lambda_N, \text{ and } \lambda_1 < 1 < \mu_1, \tag{33}$$

$$(S - \lambda_1)(P_1(S) - P_1(\lambda_1)) < 0, \text{ for } S \neq \lambda_1, \tag{34}$$

where $P_1(S)$ is defined by (12). Assume that there exist constants $\alpha_i > 0$ for each $i \geq 2$ satisfying $\lambda_i < 1$, such that

$$\max_{0<S<\lambda_1} g_i(S) < c_i < \min_{\lambda_i<S<\rho_i} g_i(S), \tag{35}$$

where $g_i(S) = \frac{f_1(S)p_i(S)}{f_i(S)p_1(S)}$ and $\rho_i = \min(\mu_i, 1)$. Then the equilibrium E_1^* is GAS for (6) with respect to the interior of the positive cone.

Proof. First, note that (34) is the same as (27), and condition $\lambda_1 < 1 < \mu_1$ in (33) is equivalent to (26). If $S < \lambda_i$ then $f_i(S) < 0$ and $f_1(S) > 0$ so that (28) is satisfied for any choice of $c_i > 0$. Similarly if $\mu_i < 1$ and $\mu_i < S < 1$ then $f_i(S) < 0$ and $f_1(S) > 0$ so that (28) is satisfied for any choice of $c_i > 0$. On the other hand, if $0 < S < \lambda_1$ then $f_i(S) < 0$ and, using $g_i(S) < c_i$ in (35), $f_1(S)p_i(S) < c_i f_i(S)p_1(S)$. Finally, if $\lambda_i < S < \rho_i$, then $f_i(S) > 0$ and, using $g_i(S) > c_i$ in (35), $f_1(S)p_i(S) < c_i f_i(S)p_1(S)$. Thus (28) is satisfied. The result follows from Theorem 2. □

5 Single species

In the case $N = 1$, using the notation $x = x_1$, (8) takes the form

$$\begin{aligned} S' &= 1 - S - xp(S), \\ x' &= f(S)x. \end{aligned} \tag{36}$$

Let $S = \lambda$ be the smallest positive value of S such that $f(S) = 0$ and $x^* = P(\lambda)$ with $P(S)$ defined by $P(S) = \frac{1-S}{p(S)}$ as in (12). If $\lambda < 1$, then $E^* = (\lambda, x^*)$ is a positive equilibrium. Assume that $f'(\lambda) > 0$ and $P'(\lambda) < 0$, so that E^* is locally asymptotically stable. We consider the global asymptotic stability of E^*.

Corollary 4 (Theorem 2.11 in [2] or Lemma 2.3 in [17]). *Assume that $\lambda < 1$ and for all $0 < S < 1$,*

$$(S - \lambda)f(S) > 0, \text{ for } S \neq \lambda, \tag{37}$$

$$(S - \lambda)(P(S) - P(\lambda)) < 0, \text{ for } S \neq \lambda. \tag{38}$$

Then the equilibrium E^* is GAS for (36) with respect to the interior of the positive cone.

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Proof. Notice that (37) is the same as (13) or (26) and (38) is the same as (14) or (27). Since for $N = 1$, condition (15) in Theorem 1 or condition (28) in Theorem 2 is trivially satisfied, the result is a corollary of Theorem 1 or Theorem 2. □

Corollary 4 was obtained by Arino, Pilyugin and Wolkowicz (see [2], Theorem 2.11). Using the Lyapunov function

$$V_{APW} = \frac{1-\lambda}{p(\lambda)} \int_{\lambda}^{S} \frac{f(\sigma)}{1-\sigma} d\sigma + \int_{x^*}^{x} \frac{\xi - x^*}{\xi} d\xi, \tag{39}$$

these authors proved that if

$$1 - \frac{p(S)(1-\lambda)}{p(\lambda)(1-S)} \text{ has exactly one sign change for } 0 < S < 1 \tag{40}$$

then E^* is GAS. Notice that (40) is equivalent to (38). In the single species case, our Lyapunov function (17), used in the proof of Theorem 1, reduces (up to a constant) to the Lyapunov function V_{APW} considered in [2]. Corollary 4 was obtained also by Pilyugin and Waltman (see [17], Lemma 2.3). Using the Lyapunov function

$$V_{PW} = \int_{\lambda}^{S} \frac{f(\sigma)}{p(\sigma)} d\sigma + \int_{x^*}^{x} \frac{\xi - x^*}{\xi} d\xi, \tag{41}$$

these authors proved that if

$$S = \lambda \text{ is the only zero of } R(S) = 1 - S - x^* p(S) \tag{42}$$

then E^* is GAS. Notice that (42) is equivalent to (38). In the single species case, our Lyapunov function (25), used in the proof of Theorem 2, reduces to the Lyapunov function V_{PW} considered in [17].

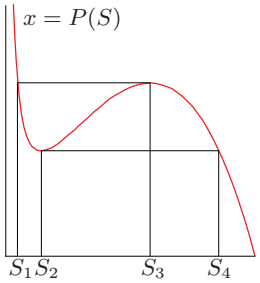

Figure 1: The graph of the function $x = P(S)$ showing the values S_1, S_2, S_3 and S_4.

Notice that the isoclines $S' = 0$ and $x' = 0$ of (36) are given by

$$S' = 0 \Longleftrightarrow x = P(S),$$

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$$x' = 0 \Longleftrightarrow x = 0 \text{ or } S = \lambda.$$

If the vertical line $S = \lambda$ intersects the curve $x = P(S)$ on an increasing arc, then, from Lemma 1, the intersection is an unstable equilibrium point E^*. Using Poincaré-Bendixon theory we can show that the system has at least a periodic orbit surrounding the equilibrium. Otherwise, if the vertical line $S = \lambda$ intersects the curve $x = P(S)$ on an decreasing arc, then, from Lemma 1, E^* is locally asymptotically stable. The condition (38) has the following graphical interpretation: if E^* is the only intersection of the isocline $x = P(S)$ with the horizontal line $x = x^*$ then E^* is GAS. For instance, in the situation depicted on Fig. 1, the function $x = P(S)$ has two critical points $S = S_2$ and $S = S_3$. Let S_1 and S_2 defined by $P(S_1) = P(S_3)$ and $P(S_4) = P(S_2)$ respectively. Then,

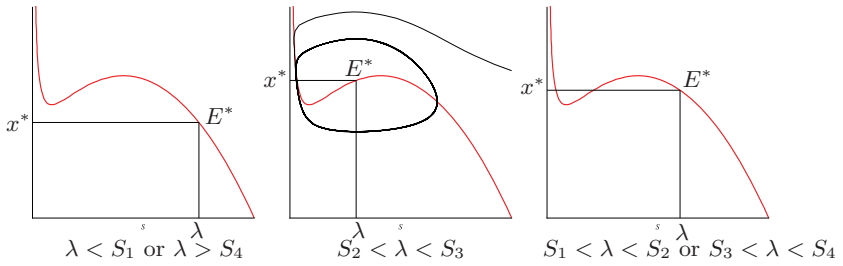

Figure 2: If $\lambda < S_1$ or $\lambda > S_4$, the equilibrium point E^* is GAS. If $S_2 < \lambda < S_3$ then, the system admits at least one limit cycle. If $S_1 < \lambda < S_2$ or $S_3 < \lambda < S_4$ the condition (38) does not hold and Corollary 4 cannot be applied.

see Fig 2:

Case 1. If $0 < \lambda < S_1$ or $S_4 < \lambda < 1$ then E^* is the only intersection of the isocline $x = P(S)$ with the horizontal line $x = x^*$. Thus, using Corollary 4, the equilibrium E^* is GAS.

Case 2. If $S_2 < \lambda < S_3$ then, using Lemma 1, the equilibrium E^* is unstable. The system admits at least one limit cycle.

Case 3. If $S_1 < \lambda < S_2$ or $S_3 < \lambda < S_4$ then, using Lemma 1, the equilibrium E^* is locally asymptotically stable. The horizontal line $x = x^*$ has three intersections with $x = P(S)$. Since (38) does not hold, we cannot conclude if the equilibrium is GAS or not.

We illustrate the third case by an example taken from [17]. Consider (36) with

$$p(S) = \frac{q(S)}{y(S)}, \quad f(S) = q(S) - D, \text{ where } q(S) = \frac{aS}{b+S}, \quad y(S) = 1 + cS^2,$$

corresponding to Monod growth function and quadratic yield. Let $D_2 = q(S_2)$ and $D_3 = q(S_3)$. For the parameter values given in the caption of Fig. 3, and $D > D_3$ and close to D_3, the equilibrium point E^* is exponentially stable and it

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is surrounded by two limit cycles. Actually, the limit cycle which exists for all $D_2 < D < D_3$ disappears for some critical $D_c > D_3$ through a subcritical Hopf bifurcation. For more details and explanations the reader is referred to [17].

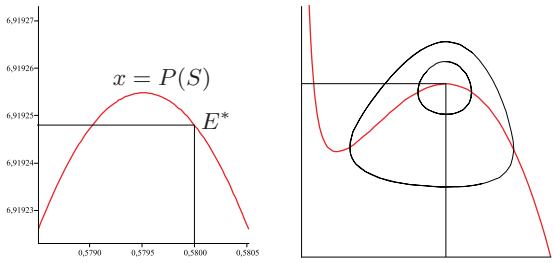

Figure 3: If $D = 1$ the system has two limit cycles. On the center of the figure an enlargement of the graph shows that the equilibrium point $E^* = (\lambda, x^*)$ lies on a decreasing branch of the graph of the function $x = P(S)$. For the parameters values $a = 2$, $b = 0.58$ and $c = 46$: $S_1 \simeq 0.048$, $S_2 \simeq 0.143$, $S_3 \simeq 0.579$, $S_4 \simeq 0.855$ and $\lambda = 0.58$. Hence $S_3 < \lambda < S_4$.

The case $N = 1$ of a single species can also be investigated with the Bendixon-Dulac criterion. As shown in [7], using the variable $y = \log(x)$, (36) is written

$$\begin{aligned} S' &= 1 - S - e^y p(S), \\ y' &= f(S), \end{aligned} \tag{43}$$

with resulting divergence

$$\text{div} = -1 - e^y p'(S).$$

If $p'(S) > 0$ then the divergence is negative and no periodic solution can exist. Poincaré-Bendixon theorem shows that convergence to the equilibrium E^* ensues. Thus E^* is GAS under the conditions $p' > 0$ and (37). This result is a consequence of Corollary 4, since the condition $p'(S) > 0$ implies $P'(S) < 0$ for $0 < S < 1$ and hence, (38) holds. However, the condition (38) in Corollary 4 can accept slightly negative p', since $P'(S) < 0$, for $0 < S < 1$, is equivalent to $p'(S) > \frac{-p(S)}{1-S}$, for $0 < S < 1$.

6 Monod growth functions and linear yields

Models with linear yields were biologically motivated by [1, 5, 6] who noticed the existence of limit cycles for some values of the parameters. The rigorous mathematical study was given in [17]. Consider the particular case of (1), where the growth functions $q_i(S)$ are given by (10), and the yields $y_i(S) = q_i(S)/p_i(S)$ are linear

$$y_i(S) = Y_i(1 + c_i S)$$

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where $Y_i > 0$ and $c_i \geq 0$. System (1), with $D = 1$ and $S^0 = 1$, takes the form

$$\begin{aligned} S' &= 1 - S - \sum_{j=1}^{N} \frac{a_j S}{b_j + S} \frac{x_j}{Y_j(1 + c_j S)}, \\ x_i' &= \left[\frac{a_i S}{b_i + S} - D_i \right] x_i, \qquad\qquad i = 1 \cdots N. \end{aligned} \tag{44}$$

The break-even concentrations λ_i are given by (30). In this section we give analytical conditions on the parameters of (44) so that conditions (13), (14) and (15) are satisfied and Theorem 1 can be applied. We need the following

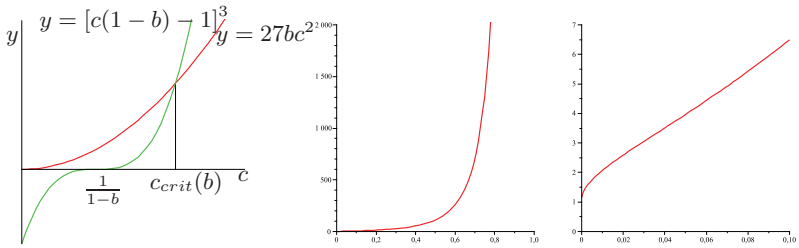

Figure 4: On the left: the definition of the function $c_{crit}(b)$. For each $b < 1$, the functions $y = [c(1-b)-1]^3$ (in green) and $y = 27bc^2$ (in red) intersect for $c = c_{crit}(b)$. On the center, the numerical plot (in red) of the function $c = c_{crit}(b)$. On the right, the behaviour of this function for small values of b.

technical result.

Lemma 7. *The function* $Q(S) = \frac{(1-S)(b+S)(1+cS)}{S}$ *is decreasing over* $[0,1]$ *if and only if*

$$[c(1-b)-1]^3 \leq 27bc^2.$$

This condition is equivalent to either $b \geq 1$ *or* $b < 1$ *and* $c \leq c_{crit}(b)$*, where* $c_{crit}(b)$ *is the positive zero of* $[c(1-b)-1]^3 = 27bc^2$.

Proof. Since

$$Q'(S) = -\frac{2cS^3 + (1 + c(b-1))\,S^2 + b}{S^2}, \quad Q''(S) = -\frac{2\left(b - cS^3\right)}{S^2},$$

the function $Q(S)$ has an inflexion point for $S = (b/c)^{\frac{1}{3}}$. The function $Q(S)$ is nonincreasing over $[0,1]$ if and only if its derivative at the inflexion point is nonpositive, that is, $P'\left((b/c)^{\frac{1}{3}}\right) \leq 0$. Straightforward computations show that this condition is equivalent to $[c(1-b)-1]^3 \leq 27bc^2$. If $b \geq 1$ then the first term of the inequality is negative and hence the inequality if satisfied for all $c \geq 0$. If $b < 1$, then the inequality is satisfied if and only if $c \leq c_{crit}(b)$, see Fig. 4. □

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The expression of $c_{crit}(b)$ can be obtained by Cardan formulas. Notice that $c_{crit}(0) = 1$ and $c_{crit}(b)$ is increasing with b, see Fig. 4.

Theorem 3. *Assume that*

$$\lambda_1 < \lambda_2 \leq \cdots \leq \lambda_N, \qquad \lambda_1 < 1, \tag{45}$$

$$\textit{either } b_1 \geq 1 \textit{ or for each } i \geq 1 \textit{ satisfying } \lambda_i < 1,\ c_i \leq c_{crit}(b_1). \tag{46}$$

Then the equilibrium E_1^* is GAS for (44) with respect to the interior of the positive cone.

Proof. Let us prove that (13), (14) and (23) hold. The Monod function $f_1(S)$ is increasing. Hence, (13) holds. The function $P_1(S)$ is

$$P_1(S) = \frac{(1-S)(b_1+S)(1+c_1S)}{S}.$$

By Lemma 7, it is decreasing if and only if either $b_1 \geq 1$ or $b_1 < 1$ and $c_1 \leq c_{crit}(b_1)$. Hence, (14) holds. For each $i \geq 2$, the function $g_i(S)$ defined by (22) is

$$g_i(S) = \frac{f_i(S)}{f_1(S)}\frac{1-S}{p_i(S)} = \frac{Y_i}{a_i}\frac{a_i - D_i}{a_1 - D_1}\frac{S-\lambda_i}{S-\lambda_1}Q_i(S)$$

where $Q_i(S) = \frac{(1-S)(b_1+S)(1+c_iS)}{S}$. Assume that (46) holds. By Lemma 7, the function $Q_i(S)$ is decreasing. Therefore,

$$\min_{0<S\leq\lambda_1} Q_i(S) = Q_i(\lambda_1) > Q_i(\lambda_i) = \max_{\lambda_i\leq S<1} Q_i(S).$$

Since $\lambda_1 < \lambda_i$, the function $S \mapsto \frac{S-\lambda_i}{S-\lambda_1}$ is increasing. Therefore,

$$\min_{0<S\leq\lambda_1} \frac{S-\lambda_i}{S-\lambda_1} = \frac{\lambda_i}{\lambda_1} > 1 > \frac{1-\lambda_i}{1-\lambda_1} = \max_{\lambda_i\leq S<1} \frac{S-\lambda_i}{S-\lambda_1}.$$

Thus,

$$\min_{0<S<\lambda_1} g_i(S) \geq \frac{Y_i}{a_i}\frac{a_i - D_i}{a_1 - D_1} \min_{0<S<\lambda_1} \frac{S-\lambda_i}{S-\lambda_1} \min_{0<S<\lambda_1} Q_i(S) > \frac{Y_i}{a_i}\frac{a_i - D_i}{a_1 - D_1}Q_i(\lambda_1),$$

and

$$\max_{\lambda_i<S<1} g_i(S) \leq \frac{Y_i}{a_i}\frac{a_i - D_i}{a_1 - D_1} \max_{\lambda_i<S<1} \frac{S-\lambda_i}{S-\lambda_1} \max_{\lambda_i<S<1} Q_i(S) < \frac{Y_i}{a_i}\frac{a_i - D_i}{a_1 - D_1}Q(\lambda_i).$$

Hence (23) holds. The result follows from Theorem 1. □

Theorem 3 extends Corollary 2 which corresponds to the case where the yields are constant. Indeed, (45) is the same as (31) and, for constant yields, $c_i = 0$, so that the conditions (46) in Theorem 3 are satisfied. Notice that (46) is a sufficient and not necessary condition for the existence of a gap between the minimum of $g_i(S)$ over $(0, \lambda_1)$ and its maximum over $[\lambda_i, 1]$. For instance, for

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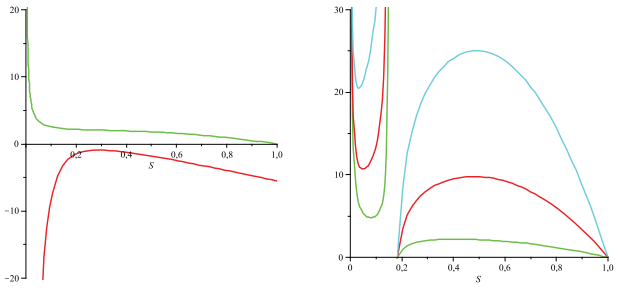

Figure 5: The graphical depiction of conditions (14) and (23) in the proof of Theorem 3. The parameter values are $c_1 = 4$, $b_1 = 0.1$, $a_1 = 1$, $b_2 = 0.15$, $a_2 = 1$ $D_1 = 0.6$ and $D_2 = 0.55$. Hence $\lambda_1 = 0.15$ and $\lambda_2 \simeq 0.18$. On the left, the function $P_1(S)$ (in green) and its derivative (in red) showing that P_1 is decreasing and so (14) is satisfied. On the right, the function $g_2(S)$ for $c_2 = 5$ (in red), $c_2 = 30$ (in green) and $c_2 = 80$ (in cyan). The condition (23) is satisfied for $c_2 = 5 < c_{crit}(0.1)$ and $c_2 = 30 > c_{crit}(0.1)$. It is not satisfied for $c_2 = 80$. Here $c_{crit}(0.1) \simeq 6.5$, see Fig. 4.

the parameter values given in the caption of Fig. 5, if $c_2 = 30 > 6.5 \simeq c_{crit}(0.1)$, there exists such a gap, see Fig. 5. Therefore, Theorem 1 applies and predict that the equilibrium is GAS, even if Theorem 3 does not apply, since $b_1 = 0.1 < 1$ and $c_2 = 30 > 6.5 \simeq c_{crit}(0.1)$. However, for $c_2 = 80 > 6.5 \simeq c_{crit}(0.1)$, there is no gap, see Fig. 5. Therefore, neither Theorem 1 nor Theorem 3 can be used. However, in each particular example it is very easy to depict graphically the conditions (13), (14) and (15) of Theorem 1 and to see if Theorem 1 can be applied or not.

7 Discussion

We briefly survey some CEP results for (5). In the Monod case [16] when the growth functions are of form (10), and assuming equal removal rates for S and all species, i.e. $D_i = D$ for $i = 1 \cdots N$, Hsu, Hubbell and Waltman [11] proved the following CEP: every solution of (5) with positive initial condition satisfies

$$\lim_{t\to\infty} S(t) = \lambda_1, \quad \lim_{t\to\infty} x_1(t) = Y_1(S^0 - \lambda_1), \quad \lim_{t\to\infty} x_i(t) = 0, \ i \geq 2,$$

under the additional assumption $0 < \lambda_1 < S^0$ and $\lambda_1 < \lambda_i$ for $i = 2 \cdots N$. The predictions in [11] were tested in the laboratory by the experiments of Hansen and Hubbell [8]. Similar experiments could be performed to test the predictions using microorganisms known to have variable yields. See [1, 2, 5, 6, 17] for examples of such microorganisms.

Hsu [9] used the Lyapunov function (24) to give a simple and elegant proof of the result in [11] for the case of different removal rates D_i (see Corollary

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2). Wolkowicz and Lu [25], used the Lyapunov function (16) and extended the results of [9] by allowing more general growth functions. They identified a large class of growth functions, where the constant c_i in (16) can always be found. As claimed by Smith and Waltman [22], despite the fact the c_i cannot be found for all growth functions, the work of Wolkowicz and Lu [25] represents a major step in the extension of the result of Hsu [9] to general growth functions. In the constant yield case, the CEP has been also proved under a variety of hypotheses by Armstrong and McGehee [3], Butler and Wolkowicz [4], Wolkowicz and Xia [26] and Li [14]. The hypotheses used in the papers [3, 4, 9, 11, 14, 25, 26] are summarized in Table 1 of [13]. Lyapunov techniques in the chemostat were also used in [15, 18].

The variable yield case was considered, for $n = 1, 2$ by Pilyugin and Waltman [17], with a particular interest to linear and quadratic yields, and by Huang, Zhu and Chang [12]. The general model (1) for N species, was considered by Arino, Pilyugin and Wolkowicz [2]. As noticed by these authors (see [2], Section 3), in the case of constant yields (5), including the yield terms Y_i in the substrate equation, as in (5), is mathematically equivalent to including the reciprocal in the microorganism equation instead. Indeed, (5) can be written

$$\begin{aligned} S' &= D[S^0 - S] - \sum_{j=1}^{N} p_j(S)x_j, \\ x_i' &= [Y_i p_i(S) - D_i]x_i, \qquad i = 1 \cdots N, \end{aligned}$$

where $p_i(S) = \frac{q_i(S)}{Y_i}$. Since Y_i are constant, the uptake terms p_i and growth terms q_i have the same monotonicity properties. Formally, the model (1) with yields (4) can be written

$$\begin{aligned} S' &= D[S^0 - S] - \sum_{j=1}^{N} \frac{q_j(S)}{y_j(S)}x_i, \\ x_i' &= [q_i(S) - D_i]x_i, \qquad i = 1 \cdots N, \end{aligned} \tag{47}$$

where $q_i(S)$ are the growth functions, or equivalently,

$$\begin{aligned} S' &= D[S^0 - S] - \sum_{i=j}^{N} p_j(S)x_j, \\ x_i' &= [y_i(S)p_i(S) - D_i]x_i, \qquad i = 1 \cdots N, \end{aligned} \tag{48}$$

where $p_i(S)$ are the uptake functions. One of the important differences in the case that the yields are not constant is that the variable yield terms can lead to uptake and growth functions that have now different monotonicity properties. Moreover, in the case of constant yields, the yields terms Y_i can be eliminated in (5) simply by passing to the variables $u_i = Y_i x_i$. We obtain

$$\begin{aligned} S' &= D[S^0 - S] - \sum_{j=1}^{N} q_j(S)u_j, \\ u_i' &= [q_i(S) - D_i]u_i, \qquad i = 1 \cdots N. \end{aligned}$$

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This change of variables means that we have changed the units in which the microorganisms were evaluated. There is no such trick to eliminate the yields terms in (47) of (48). Therefore, careful attention to the interpretation of the yield terms resulting in their correct placements in the equations is necessary. For details and complements, the reader is referred to [2], Section 3.

In the variable yield case, the CEP has been proved for (1), under some technical conditions on the function p_i and q_i, by Sari [20] and Sari and Mazenc [21] (see Corollary 1 in Section 3 and Corollary 3 in Section 4). It was also shown in [21] how Corollary 3 can be fruitfully used to analyze the stability properties of systems whose yield functions depend on the variable S. For instance, the CEP holds (see Corollary 5 in [21]) for the Monod model with constant yields replaced by either linear or quadratic functions of S, and under certain additional technical assumptions. Another application is given by the following model

$$\begin{aligned} S' &= 1 - S - \tfrac{2S}{0.7+S}\tfrac{x_1}{1+cS^3} - \tfrac{m_2 S}{6.5+S}\tfrac{x_2}{120} \\ x_1' &= [\tfrac{2S}{0.7+S} - 1]x_1 \\ x_2' &= [\tfrac{m_2 S}{6.5+S} - 1]x_2. \end{aligned}$$

This model was used by Pilyugin and Waltman [17] to demonstrate that a periodic orbit was possible in the variable yield case. In this model, with two species, where one yield is constant and the other is cubic in S, it is shown in [21] that for some values of the parameters the CEP holds (see Corollary 6 in [21]).

The problem of the existence of limit cycles in chemostat equations is not always well understood [19]. In the case of constant yields, numerical simulations of model (5) have only displayed competitive exclusion. Our results concern also the case of variable yields, for which it is known [2, 12, 17] that more exotic dynamical behaviors, including limit cycles and chaos, are possible. Thus in the case of variable yields, it is of great importance to have criteria ensuring the global convergence to an equilibrium with at most one surviving species. The reader interested in biological motivations for the dependence of the yields on the substrate, may consult [2, 17] and the references therein.

The exclusion of periodic orbits in system (8) was obtained by Fiedler and Hsu (see Theorem 1.1 in [7]) under the following conditions: for all $1 \leq i \neq j \leq N$, and $0 < S < 1$

$$(S - \lambda_i) f_i(S) > 0, \quad \text{for } S \neq \lambda_i, \tag{49}$$

$$f_i(S) < 1 + f_j(S) + (1 - S)p_j'(S)/p_j(S). \tag{50}$$

Even if the result in [7] does not show the convergence to an equilibrium, it is interesting to compare the constraints on the functions f_i and p_i of [7] with our constraints. Actually, (49) is stronger than (13), since our assumption requires (49) only for f_1 and allows the f_i, for $i \neq 1$, to have other zeros than λ_i in $]0, 1[$. Let us compare the constraints on f_i and p_i imposed by the inequalities (50) to the constraints imposed by hypothesis (15): notice that (50) is a set of

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$\frac{N(N-1)}{2}$ conditions, while (15) is a set of at most $N-1$ conditions. Moreover, the constants α_i in the conditions (15) give more flexibility to these conditions. For instance, (15) are satisfied by arbitrary Monod growth functions and also by a large class of growth functions as it was shown in [21, 25]. On the other hand, (50) are not satisfied by arbitrary Monod functions, see formulas (6.10) and (6.11) in [7]. Hence the result in [7] does not recover the CEP, even in the classical and well established case of Monod functions and equal removal rates [3]. However our theorem recovers a lot of results of the existing literature.

For the purpose of comparison between our result and the result of Fiedler and Hsu [7], we just mentioned two caveats on Theorem 1.1 in [7]: first, this theorem does not recover many of the biologically interesting classical examples where the CEP is known to hold, and second, it does not prove the convergence to an equilibrium. These caveats were already mentioned in [7], Section 6. Another caveat must be signaled. Fiedler and Hsu claimed (see [7], Section 6) that, in the case $N = 1$ of a single species, condition (50) holds trivially and there is no periodic orbit for system (36). It should be noticed that condition (49) is not sufficient to exclude periodic orbits. Of course, if $p'(S) > 0$, then the Bendixon-Dulac criterion can be applied to exclude periodic orbits (see Section 5). This assumption on the monotonicity of p is not explicitly stated in Theorem 1.1 in [7]. Moreover, the condition $p'(S) > 0$ would not be satisfactory from the biological point of view. Indeed, a variable yield term $y(S) = q(S)/p(S)$ can lead to nonmonotone uptake term $p(S)$ even if the growth term $q(S)$ is monotone (see Section 5).

Fiedler and Hsu, see Section 6 in [7], claimed that the construction of Lyapunov functions in [3, 9, 14, 25, 26] strictly depends on the proportionality $p_i(S) = q_i(S)/Y_i$ required in equations (5). In Section 4, we showed how the Lyapunov function used by Hsu himself [9] for the Monod case, more than thirty years ago, can be extended to the case of (6), where growth rates are not required to be proportional to food uptake (see Theorem 2, in Section 4). For that reason, the direct proof of Theorem 2, using the extension (25) of the Lyapunov function of Hsu [9], seems to be interesting in itself. Thus, we decided to give Theorem 2 and its direct proof, despite the fact that this theorem is a corollary of Theorem 1 (see Proposition 1 in Section 4).

We list some references to the existing literature which inspired our approach. The Lyapunov function (25) used in the proof of Theorem 2 was introduced in [21] as an extension of the Lyapunov function (24) that Hsu used in [9] in the Monod case (Theorem 3.3 in [9]). In the case of one species, this Lyapunov function is equal to the function (41) used by Pilyugin and Waltman (Lemma 2.3 in [17]), as shown in Section 5. It is also a multiple of the Lyapunov function that Ballyk, Lu, Wolkowicz and Xia used in [26], page 1039 or [24], Section 3.3 (see Section 3.2 in [21]). The Lyapunov function (17) used in the proof of Theorem 1 was introduced in [20] as an extension of the Lyapunov function (16) that Wolkowicz and Lu used in [25] in the constant yields case (Theorem 2.3 in [25]). In the case of one species, it is a multiple of the Lyapunov function (39) used by Arino, Pilyugin and Wolkowicz (Theorem 2.11 in [2]), as shown in

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Section 5.

In this work, we have analyzed a general model of the chemostat with several species competing for a substrate, under the assumption that uptake rates and growth rates are not proportional. Each species is characterized by its specific growth rate, its specific removal rate, and its variable yield. Our study reveals that the CEP holds for a large class of systems: the species with the smallest break-even concentration can be the winner of the competition if some supplementary conditions, involving the uptake and growth functions are satisfied. Hence, even if the break-even concentration are depending only on the growth rates and not on the yields functions, the issue of competition really depends on the yield functions. For instance, if one on the species exhibits a linear yield, and if the parameter in the yield is enlarged, then the equilibrium, where only the winning species survives, can be destabilized, and oscillatory coexistence of more than one species becomes possible.

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